

## Primate Natal Coats: A Preliminary Analysis of Distribution and Function

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**ABSTRACT** Pelage coloration of infants was compiled for 138 species of primates. Three functional hypotheses—alloparental, infant defense, and paternity cloak—for primate natal coats are tested. Neonatal pelage contrasted with adult pelage in over half of the species examined. Subtle or inconspicuous contrast was more common than flamboyant contrast. Natal coats began to change at 5.7 weeks and disappeared by 18.0 weeks postpartum on average. The first body part to lose natal coloration was the head and/or dorsum in the majority of species. Functional analyses provided no support for the only published hypothesis—alloparental—while providing partial support for two new hypotheses—infant defense and paternity cloak. A significant association between testes weight and natal coat contrast supports a link between mating system and infant contrast. This is discussed in terms of infanticide avoidance. Natal coats are proposed to be categorically differentiated into inconspicuous and flamboyant types, not differentiated by a continuous gradation, such as color. Subspecific differentiation and patterns of shared ancestry are assessed. *Am J Phys Anthropol* 104:47–70, 1997.

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Pelage color in mammals is generally believed to be adapted to predator avoidance, thermoregulation, and/or sociosexual signaling (Hershkovitz, 1977; Hope and Godfrey, 1989; Litvaitis, 1991). Primates display extreme interspecific variation in pelage coloration from silver-white to deepest black. The brilliant coloration of some primate species' pelage may reflect a reduction in anti-predator function followed by an elaboration of use for sociosexual signaling (Hershkovitz, 1977). Support for this idea may derive from the generally brighter coloration of arboreal species within families (e.g., *Pongo pygmaeus* vs. *Gorilla gorilla*; *Presbytis rubicunda* vs. *Semnopithecus entellus*; personal observation; see Hrdy, 1976).

However, neonates of many primate species differ markedly from adults in color. The molting of age-specific pelage is common

among mammals as the texture, thickness, and/or shade of immature pelage changes during ontogeny (Hershkovitz, 1977). Differences between adults and immatures are often due to the accumulation of secondary sexual characteristics in early adulthood (e.g., colored vibrissae, crests, manes, and facial marks). For example, the conspicuous facial markings of the cercopithecines typically do not develop until the juvenile stage or later (Kingdon, 1988). Yet the adoption of sharply contrasting coloration in immatures is rare in mammals as a whole. The loss of one coat and adoption of a wholly different coat in late infancy is clearly not a result of the accumulation of secondary sexual char-

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acteristics. The natal coat cannot therefore be regarded as a precursor to which adult features will be added.

The natal coat can make young infants conspicuous at great distances at a time when 1) they are maximally vulnerable to predation and 2) their social interactions are passive, infrequent, and limited in scope. Distinct coloration may call attention to a neonate and raise the risk of predation through the "oddity effect" (Curio, 1976; Landeau and Terborgh, 1986), or it may signal to conspecifics the presence of an infant at the age of maximum vulnerability to infanticide. For these reasons, the cost of conspicuous coloration may be high. However, no data are available to assess this cost. Yet the appearance, in many species, of a clearly differentiated, morphological trait in one life stage and its subsequent disappearance argues against nonfunctional explanations based on by-products of other structures (Gould and Lewontin, 1979). The widespread nature and persistence of natal coats therefore requires a functional explanation.

In this paper, I report the results of a literature search for information on natal coats and a survey questionnaire distributed to 40 zoological facilities with recent primate births. A ranking of contrast between adults and unweaned infants is devised along the lines suggested by Hrdy (1976). Data on the age at which the natal coat both began to change and completed the transition to adulthood are compiled from zoo-keepers' records and the literature. Three hypotheses for the adaptive function of natal coats are tested.

Only one functional hypothesis for marked age-related coat color variation has been proposed so far. The alloparental hypothesis, based on a conjecture put forward by Hrdy (1976), suggests that the flamboyant coats seen in some species of the subfamily Colobinae act to promote infant care by group members other than the mother. Formally stated, the alloparental hypothesis claims that natal coats evolved in infants to promote care by group members. I include a recent clarification of this view (Horwich and Gebhard, 1986), namely that motivation to carry and care for infants is released

by the natal coat rather than created by it. The natal coat offers a selective advantage by facilitating adoption if the mother dies, rescue if the mother is absent, and/or socialization through contact with others. Operationally, species displaying alloparental care of infants are more likely to display natal coats than those without alloparental care. Support for this hypothesis requires an association between the presence or intensity of alloparental care and the distribution of natal coats.

The next two functional hypotheses are predicated on the importance of infanticide avoidance in many species of primates. Although there is still debate over the evolutionary importance of infanticide (Hrdy et al., 1995; Sussman et al., 1995), incontrovertible evidence of its severity in several populations (Hiraiwa-Hasegawa, 1987; Hrdy et al., 1995; Struhsaker and Leland, 1987) and its widespread distribution (Hrdy, 1979; Treves, in press) require that one consider it a potential selective agent. Moreover, quantitative data are now accumulating on the demographic and individual behavioral changes caused by severe conspecific threat (Treves, 1996; Treves and Chapman, 1996).

The infant defense hypothesis is a modification of the alloparental hypothesis, adapted from work on black-and-white colobus (*Colobus guereza*) (Oates, 1977). Oates (1977) argued that the completely white natal coat of *C. guereza* infants encourages infant handling by nonmothers and that this in turn may protect infants from infanticidal males. The difference between the infant defense hypothesis and its predecessor is that the infant's natal coat is proposed to represent a signal to outsiders rather than to the caretakers within the group. Strange males are a potent threat to infants in many species of primates (for review see Hrdy, 1977; Hrdy et al., 1995; Struhsaker and Leland, 1987; Treves, in press). According to the infant defense hypothesis then, the infant coloration signals that group members will mount a vigorous defense against threatening males. Contrary to early views, coalitionary defense against infanticidal attacks can be quite effective (McComb et al., 1993; Smuts and Smuts, 1993; Treves and Chapman, 1996). If outside males survey groups

TABLE 1. Three functional hypotheses for the evolution of primate natal coats

	Alloparental	Infant defense	Paternity cloak
Function	Promotes infant care among nonmothers	Signals cooperative defense of infants	Obscures clues to paternity of infants
Predicted distribution	Appears in species with infant transfer	Appears in species with little promiscuity	Appears in species with promiscuous matings
Timing of change	Natal coat lost postweaning	Natal coat lost as infanticide risk declines	Natal coat lost as infanticide risk declines
First body part to change	No prediction	Ventral surfaces	Dorsal surfaces
Color	No prediction	Two functional types expected	Contrast with adult male expected

prior to initiating a takeover, they may associate the infant's coloration with extra resistance mustered by caretakers and choose another group instead.

Threatening males may be nongroup males or those who are socially peripheral to the family of the infant despite being associated with the group. As there are two types of threatening males, two types of natal coat may occur. In this view, bright natal contrast is the best long-distance signal (intended for nongroup males), whereas muted contrast communicates effectively within the group. Operationally, bright natal coats are expected in species facing a regular risk of takeovers and infanticide by nongroup males, whereas distinct yet muted natal coats will evolve in species exhibiting infanticide by individuals within the group. The last body parts to change will be those most exposed (effective for signaling) in clinging infants (crown of head and dorsum).

Finally, the paternity cloak hypothesis focuses on the difference between the pelage color of adult and infant. To reduce the risk of male-initiated infanticide, infants should display as few indications of paternity as possible. Coat color is an important visual cue for kin recognition in several mammals (Caro and Durant, 1991; Ruiz-Miranda, 1993). Among mantled howlers (*Alouatta palliata*), a male with unusual foot coloration was observed to kill several infants but spared an infant with similar foot coloration (Clarke, 1983). In this view, natal coats are an infant strategy operating to circumvent paternity discrimination mechanisms of adult males. Facing a completely different pelage, a male may be unable to identify phenotypic markers which exclude or confirm paternity by comparison with his own appearance or that of other males. Unable to

assign or exclude paternity, he may be less likely to commit infanticide. Completely unfamiliar males who have not mated with group females will not heed such signals, so social systems in which males gain sole reproductive access should not evolve natal coats. Put another way, systems with multiple mating favor the evolution of natal coats, because associated males have a finite probability of fathering offspring and therefore some reason to discriminate nonkin from kin.

Operationally, infants in groups with promiscuous mating systems will be more likely to have natal coats, and those body parts which are subject to phenotypic matching will have natal coloration for the longest periods. Conversely, the first body parts to change will be those which are invisible to the male (his own back, head, and face), because, unable to see his own phenotype, the male cannot discriminate against infants even if they resemble other males in the group.

The three hypotheses and their predictions are summarized in Table 1.

#### DISTINGUISHING THE HYPOTHESES

Superficially, the infant defense and paternity cloak hypotheses are neatly opposed: infant defense predicts that takeovers by nongroup males (a characteristic of one-male groups) lead to selection for natal coats, while paternity cloak predicts that promiscuity (a characteristic of multimale groups) triggers selection for natal coats. In one-male social groups, paternity cloak predicts no benefit to hiding paternity, because most males never mate with group females until they take over a group, providing no need for paternity discrimination. In contrast, the infant defense hypothesis predicts bright infant coloration as a long-distance

signal in such societies. Unfortunately, this simple dichotomy is misleading.

First, takeovers or rank reversals by strange males are not restricted to one-male groups but may occur in multimale groups of many different types (Bercovitch, 1988; Borries, in press; Camperio Ciani, 1984; Pope, 1990; Struhsaker and Leland, 1985; Tarara, 1987). Thus, signals to nongroup or peripheral males as required by infant defense may also be helpful in multimale social systems.

Second, promiscuity is by no means restricted to multimale groups. Nongroup males may sneak copulations with females peripheral to a one-male group (Clarke, 1983; Jones and Bush, 1988), or actually invade a one-male group en masse to copulate (Cords, 1988; Rowell, 1988; Struhsaker, 1988). Thus, the long-term presence of a single male in a group provides little assurance that the resident has 100% paternity certainty. For example, one-male groups of patas monkeys (*Cercopithecus patas*) have a complex pattern of paternity (Ohsawa et al., 1993), which may place some pressure on a resident male to discriminate against unrelated infants. This may also reduce the tendency of nongroup males to act infanticidally.

Third, some multimale groups are characterized by nearly exclusive mating by one male or clear pairing between males and females (Boinski, 1987; Janson, 1984; Pope, 1990; van Schaik and Kappeler, 1993; Watts, 1992). Thus, multimale structure is not a reliable indicator of promiscuity.

As a result, a simple categorization of social systems based on group composition is inadequate without a clearer picture of female mating behavior. Unfortunately, it is difficult to detect outside copulations, precisely because the actors are seeking concealment (Rowell, 1988). Yet one needs an accurate measure of the frequency with which females mate multiple males in one conception cycle or season and the number of associated males who have no paternity confidence. Such data are not typically available. Therefore, an indirect measure was sought to characterize species' mating systems. The testicular volume of males is one indicator of past levels of sperm competition

and thereby of promiscuity in a species (Harcourt et al., 1995; Kappeler, 1993).

Turning back to the hypotheses and their operational tests, species with low testes mass controlled for body size (rare promiscuity) should be the same species with natal coats (according to the infant defense hypothesis) because systems with few promiscuous matings will have higher numbers of males who have no access to females and therefore pose a threat to infants. Contradicting this prediction, the paternity cloak hypothesis predicts that species with low testes mass adjusted for body size will be the species without natal coats, because higher paternity confidence (rare promiscuity) reduces the need for paternity discrimination (Table 1).

Note that in those species with related male coalitions monopolizing copulations (e.g., *Pan troglodytes*, *Procobbus colobus badius*: Struhsaker and Oates, 1975; Struhsaker and Pope, 1991; Tutin, 1975), cues to paternity will be obscured by the relatedness of the males and infanticide will be suppressed by kin selection, thus rendering natal coats less useful.

#### **TIMING AND COLORATION PREDICTIONS**

The timing of pelage change provides further differentiation of the hypotheses (Table 1). Both the paternity cloak and the infant defense hypotheses predict that natal coats will fade as the infant's vulnerability to infanticide decreases (under 1 year in most species [Sommer and Mohnot, 1985]). The alloparental hypothesis predicts that natal coats will grade into juvenile coats or will disappear when the infant is able to survive on its own (past weaning or beyond 1 year typically). Because the early juvenile phase is sometimes associated with higher mortality (Dittus, 1980), alloparental care may be beneficial far beyond weaning in some species.

Predictions about the parts of the body which lose natal coloration first are most clearly contradictory among the three hypotheses (Table 1). An animal's own dorsum and head are not subject to self-scrutiny, making them least useful for phenotypic matching. Because an adult male seeking clues to paternity is unable to inspect his own back or head efficiently, the need for

natal coloration on the infant's head and dorsum declines most swiftly, according to paternity cloak. In contrast, infant defense predicts that these body parts are the last to change because they are most often visible from a distance in a clinging infant.

No functional hypothesis predicts specific colors of natal coats. However, the general claim made by Hrdy (1976) that species with heavy predation pressure will avoid flamboyant contrasts is expected to influence natal color regardless of the function of the coat. Infant defense predicts only that infants will contrast with adults so colors serve as visual signals of varying detectability over distance: one-male groups will have brighter coloration than multimale groups. Paternity cloak predicts that natal coats will obscure telltale adult male markings, without specifying color (Table 1).

### METHODS

The objectives of this data collection were to document 1) the distribution and phylogenetic pattern of natal coat coloration in Primates and 2) the ontogeny of natal coat change. Information on primate natal coats was taken from two sources: the primate literature and the records of captive facilities. Information in the literature derived from large taxonomic reviews as well as studies in captivity and the field. Surveys were circulated to 40 zoos in North America and the British Isles (see Acknowledgments for full list of respondents). Zoos were selected if they had recorded a birth in the species of interest sometime between 1992 and 1994. Data on coloration based solely on recall by keepers were discarded unless supported by other sources. The survey circulated to zoos attempted to categorize contrasts between adults and infants using a pictorial guide as a first step toward quantifying pelage variation. Dorsal coat coloration was the primary target of contrast comparisons, but head and ventral coloration played a part in some ambiguous cases. Copies of the survey are available from the author, as are details of actual coloration not presented here.

The three categories suggested by Hrdy (1976) were used in the pictorial guides as follows.

Category 0 applied to infants who were indistinguishable from adults or whose pelage differences were within the range of adult variation. This included any pelage differences due simply to hair length, texture, or absence of obvious secondary sexual characteristics. When immatures were scored as slightly lighter or darker than adults without differences in color, no contrast was recorded. This category is referred to as *no contrast* hereafter.

Category 1 (discrete but discreet [Hrdy 1976]) applied to infants who contrasted with adults but were not themselves eye-catching. In general, dark colors (brown, grey, black, olive) fell into this category, termed *inconspicuous* henceforth. No claim is made about conspicuousness within the environment, only to contrast with the adult.

Category 2 (flamboyant [Hrdy, 1976]) applied to infants who were distinct with bright contrasting coloration. Light colors (red, orange, yellow, white) which were set against dark adults or against contrasting bright adults fell into this category. I accept the term *flamboyant* for this category.

Quantification using a pictorial guide suffers from subjectivity. For example, the facial coloration of many Callitrichidae renders adults different from immatures (Hershkovitz, 1977; personal observations). Such differences are typically due to secondary sexual traits acquired at maturity rather than natal pelage variation. Nevertheless, some observers might describe these as category 1 differences (inconspicuous). Two survey responses which were based on facial or skin coloration rather than coat coloration were recoded from 1 to 0 (see Table 2 footnote). Discrepancies or outright contradictions between different sources of information occurred in more than ten cases (Table 2). To reduce subjectivity, I used information from multiple sources whenever possible, and averages or central tendencies were sought for continuous data. Persistent ambiguity in the coding of contrast was not resolved for some entries in Tables 2 and 3.

Information is tabulated by superfamily and, within superfamilies, alphabetically by species. Some species are not represented in the data set. The data tables are organized by entries reflecting the different sources of



TABLE 2. Primate natal coat contrast compared to parents

Species <sup>1</sup>	Subspecies <sup>2</sup>	Infant contrast <sup>3</sup>		Sources <sup>6</sup>
		To mother	To father	
Ceboidae				
<i>Alouatta caraya</i>		0	2	1–3
<i>A. fusca</i>		0 or 1	1	4
<i>A. palliata</i>	<i>palliata</i>	1	1	5 contra 4
<i>A. pigra</i>		1	1	6 contra 4
<i>A. seniculus</i>	<i>macconnelli</i>	0 or 1	0 or 1	4
	<i>sara</i>	1	1	7
<i>Aotus trivirgatus</i>		0	0	8–10
<i>Ateles fusciceps</i>	<i>robustus</i>	0	0	11
<i>A. geoffroyi</i>	<i>geoffroyi</i>	2	2	12, 13
	Subspecies?	1	1	4
<i>A. paniscus</i>	<i>paniscus</i>	0 or 1	0 or 1	4
<i>Brachyteles arachnoides</i>		0 or 1	0 or 1	4, 14
<i>Cacajao melanocephalus</i>		0	0	10
<i>Callicebus moloch</i>	<i>cupreus</i>	0	0	10
<i>C. personatus</i>	<i>nigrifrons</i>	1	1	10
<i>Callimico goeldi</i>		0	0	15, 16
<i>Callithrix argentata</i>		0	0	17
<i>C. geoffroyi</i>		0	0	17
<i>C. jacchus</i> <sup>4</sup>		0	0	18, 19
<i>C. penicillata</i>	<i>kuhls</i>	0	0	7
	Subspecies?	1	1	20
<i>Cebuella pygmaea</i>		0	0	20
<i>Cebus albifrons</i>		0	0	10
<i>C. apella</i>	<i>cay</i>	0	0	21
	<i>jurnanus</i>	0	1	10
	<i>nigritus</i>	1	1	10
<i>C. capucinus</i>		0	0	10, 22
<i>C. olivaceus</i>		0	0	10
<i>Chiropotes albinasa</i>		0	0	10
<i>C. chiropotes</i>		1	1	10
<i>C. satanas</i>		1	1	10
<i>Lagothrix lagotricha</i>	<i>poepigii</i>	0	0	10, 23
<i>Leontopithecus rosalia</i>	<i>chrysopygus</i>	0	0	17, 20
	<i>rosalia</i>	1	1	20
<i>Pithecia pithecia</i>	<i>chrysocephala</i>	5	5	10
	<i>pithecia</i>	1	1	12, 25
<i>Saguinus bicolor</i> <sup>4</sup>	<i>bicolor</i>	0	0	17, 20
<i>S. fuscicollis</i>		0	0	20
<i>S. imperator</i>	<i>subgriscens</i>	0	0	7
	Subspecies?	1	1	20
<i>S. midas</i>		0 or 1	0 or 1	20, 26
<i>S. nigricollis</i>		0	0	20
<i>S. oedipus</i>		0	0	20
<i>Saimiri oerstedii</i>		0	0	10
<i>S. sciureus</i>		0	0	10, 27
Cercopithecoidea				
<i>Cercocebus galeritus</i>	<i>agilis</i>	0 or 1	0 or 1	12, 28
	<i>chrysogaster</i>	1	1	29
<i>C. torquatus</i>	<i>torquatus</i>	0 or 1	0 or 1	7, 28
	<i>atys</i>	0	0	15, 28
<i>Cercopithecus aethiops</i>	<i>pygerythrus</i>	1 or 2	1 or 2	30
	<i>sabaeus</i>	2	2	31
	<i>tantalus</i>	2	2	31
<i>C. ascanius</i>	<i>schmidtii</i>	1	1	31–33
<i>C. campbelli</i>		0	0	31
<i>C. denti</i>		1	1	31
<i>C. diana</i>	<i>diana</i>	0 or 1	0 or 1	13, 31
<i>C. dryas (salongo)</i>		1	1	34
<i>C. hamlyni</i>		2	2	31
<i>C. lhoesti</i>		1	1	31, 32
<i>C. mitis</i>	<i>boutourlinii</i>	1	1	31
	<i>mitis</i>	0	0	31
	<i>opisthostictus</i>	1	1	31
	<i>stuhlmanni</i>	1	1	13, 33 contra 31

TABLE 2. (continued)

Species <sup>1</sup>	Subspecies <sup>2</sup>	Infant contrast <sup>3</sup>		Sources <sup>6</sup>
		To mother	To father	
<i>C. mitis (albogularis)</i>	<i>francescae</i>	0	0	31
	<i>moloneyi</i>	0	0	31
	<i>kibonotensis</i>	1	1	31
	<i>kolbi</i>	1	1	31
<i>C. neglectus</i>		1	1	18, 34
<i>C. nictitans</i>	<i>nictitans</i>	0 or 1	0 or 1	13, 31
<i>C. pogonias</i>	<i>grayi</i>	0	0	35
<i>C. wolffi</i>		0	0	12
<i>C. (Allenopithecus) nigroviridis</i>		0	0	36
<i>C. (Erythrocebus) patas</i>		1 or 2	1 or 2	18, 36–38
<i>C. (Miopithecus) talapoin</i>		0	0	31, 33, 39
<i>Colobus angolensis</i>		2	2	40
<i>C. guereza</i>	<i>kikuyensis</i>	2	2	21, 36, 40
<i>C. polykomos</i>	<i>polykomos</i>	2	2	17, 40–42
<i>C. satanas</i>		1	1	40
<i>C. vellerosus</i>		2	2	40
<i>Lophocebus albigena</i>	<i>johnstoni</i>	0	0	28, 33, 43
<i>L. atterimus</i>		0	0	28
<i>Macaca arctoides</i>		2	2	44
<i>M. assamensis</i>		1	1	28
<i>M. cyclopis</i>		1	1	28
<i>M. fascicularis (irus)</i>		1	1	28, 45, 46
<i>M. fuscata</i>		0 or 1	0 or 1	19, 28, 33, 35
<i>M. hecki</i>		0	0	28, 47
<i>M. maura</i>		0 or 1	0 or 1	28, 47
<i>M. mulatta</i>		1	1	28, 46
<i>M. nemestrina</i>		1	1	28, 45
<i>M. nigra</i>	<i>nigra</i>	0	0	17, 26
	Subspecies?	0	0	7, 39, 41, 47
<i>M. nigrescens</i>		0 or 1	0 or 1	28, 47
<i>M. ochreata</i>		0 or 1	0 or 1	28, 47
<i>M. radiata</i>		1	1	28
<i>M. silenus</i>		1	1	16
<i>M. sinica</i>	<i>aurifrons</i>	1 or 2	1 or 2	28
	<i>sinica</i>	1	1	28
<i>M. sylvanus</i>		0, 1 or 2	0, 1 or 2	28, 41
<i>M. thibetana</i>		0	0	48
<i>M. tonkeana</i>		0 or 1	0 or 1	28, 47
<i>Mandrillus leucophaeus</i>		1	1	7, 49
<i>M. sphinx</i>		0 or 1	0 or 1	18, 33, 49
<i>Nasalis larvatus</i>		0	0	50
<i>Papio cynocephalus</i>		1	1	33, 49, 51
<i>P. hamadryas</i>		1	2	18, 41, 49
<i>P. papio</i>		1	1	15
<i>Presbytis comata</i>		1 or 2	1 or 2	40
<i>P. frontata (femoralis?)</i>		2	2	40, 52
<i>P. hosei</i>		1 or 2	1 or 2	40
<i>P. melalophos</i>		2	2	40, 52, 53
<i>P. potenziani</i>		2	2	40, 50, 54
<i>P. rubicunda</i>		2	2	33, 40
<i>P. thomasi</i>		1 or 2	1 or 2	40, 52
<i>Procolobus badius</i>		1	1	33, 40, 55
<i>P. verus</i>		0	0	40
<i>Pygathrix nemaeus</i>		0	0	50
<i>P. (Rhinopithecus) roxellana</i>		2	2	56
<i>Semnopithecus (Trachypithecus) cristatus</i>		2	2	21, 54
<i>S. (T.) entellus</i>	<i>hypoleucus</i>	1	1	40
	Subspecies?	2	2	33, 40, 57
<i>S. (T.) francoisi</i>		2	2	29, 58–60
<i>S. (T.) geei</i>		2	2	40
<i>S. (T.) johnii</i>		1 or 2	1 or 2	40, 50, 61
<i>S. (T.) obscurus (phayrei)</i>		2	2	15, 40, 50
<i>S. (T.) pileatus</i>		2	2	40, 62
<i>S. (T.) vetulus (senex)</i>		1	1	13, 40, 63
<i>Theropithecus gelada</i>		1	1	7, 12, 49

(Continued)

TABLE 2. (continued)

Species <sup>1</sup>	Subspecies <sup>2</sup>	Infant contrast <sup>3</sup>		Sources <sup>6</sup>
		To mother	To father	
Hominoidea				
<i>Gorilla gorilla</i>		0	0	64
<i>Hylobates</i> spp.			See Table 3	
<i>Pan troglodytes</i>		0	0	33, 65
<i>Pongo pygmaeus</i>		0	0	66
Lemuroidea				
<i>Avahi laniger</i>		1	1	67
<i>Cheirogaleus major</i>	<i>major</i>	0 or 1	0 or 1	67
<i>Eulemur (Petterus) fulvus</i>	<i>fulvus</i>	0	0	68
<i>E. (P.) macaco</i>	<i>flavifrons</i>	5	5	69, 70
	<i>macaco</i>	5	5	67, 70
	<i>sanfordi</i>	0	0	67
<i>Lemur catta</i>		0	0	67, 68, 71
<i>Microcebus murinus</i>		0	0	66
<i>Propithecus diadema</i>		0	0	66
<i>P. tattersalli</i>		0	0	71
<i>P. verreauxi</i>		1	1	67, 68
<i>Varecia variegata</i>		0	0	67
Lorisoidea				
<i>Arctocebus calabarensis</i>		0 or 1	0 or 1	67
<i>Galago crassicaudatus</i>		0	0	67
<i>G. moholi</i>		0	0	67
<i>G. senegalensis</i>		0	0	67
<i>Loris tardigradus</i>	<i>grandis</i>	0	1	67
	<i>lydekkerianus</i>	1	1	67
	<i>nordicus</i>	1	1	67
	<i>nycticeboides</i>	1	0	67
	<i>tardigradus</i>	1	1	67
<i>Nycticebus coucang</i>		0 or 1	0 or 1	46, 67
<i>N. pygmaeus</i>		1	1	67
<i>Perodicticus potto</i>	<i>edwardsi</i>	1	1	67
	<i>ibeanus</i>	1	1	67
	<i>juju</i>	0	0	67
	<i>potto</i>	0	0	67
	Subspecies?	1	1	73
Tarsioidea				
<i>Tarsius bancanus</i>		1	1	73
<i>T. syrichta</i>		0 or 1	0 or 1	73, 74

<sup>1</sup> Names within parentheses are synonymous, unresolved, or contested.

<sup>2</sup> Blank spaces for subspecies reflect lack of information or all subspecies were similar.

<sup>3</sup> Two values (e.g., 1 or 2) reflect contradictory sources or doubt as to contrast.

<sup>4</sup> Facial coloration was the primary distinction.

<sup>5</sup> Sexual dichromatism appears in neonates.

<sup>6</sup> Sources (contra appears in the citation when one source is ruled out in favor of others): 1, Riverbanks Zoo; 2, Audubon Zoo; 3, Malinow, 1968; 4, Hill, 1962; 5, Glander, 1983; 6, Horwich and Gebhard, 1986; 7, Los Angeles Zoo; 8, Hershkovitz, 1983; 9, Wright, 1984; 10, Hill, 1960; 11, Sequoia Park Zoo; 12, San Antonio Zoo; 13, Baton Rouge Zoo; 14, Strier, 1986; 15, Brookfield Zoo; 16, Cheyenne Mountain Zoo; 17, Jersey Wildlife Preservation Trust; 18, Toronto Metro Zoo; 19, Buffalo Zoo; 20, Hill, 1957; 21, Denver Zoo; 22, Dreher Park Zoo; 23, Louisville Zoo; 24, Hershkovitz, 1987a; 25, Roger Williams Park Zoo; 26, Santa Ana Zoo; 27, Hershkovitz, 1984; 28, Hill, 1974; 29, Sacramento Zoo; 30, Gartlan and Brain, 1968; 31, Hill, 1966; 32, Kingdon, 1974; 33, Treves, personal observation; 34, Colyn et al., 1991; 35, Cincinnati Zoo; 36, Woodland Park Zoo; 37, Palmer et al., 1981; 38, Chism, 1986; 39, Chester Zoo; 40, Oates et al., 1994; 41, Paignton Zoo; 42, Mearns and Pidgeon, 1978; 43, Waser, 1974; 44, Fooden, 1990; 45, Crockett and Wilson, 1980; 46, Roonwal and Mohnot, 1977; 47, Fooden, 1969; 48, Fooden et al., 1985; 49, Hill, 1970; 50, Groves, 1970; 51, Hendy, 1986; 52, Aimi and Bakar, 1992; 53, Ruhayat, 1983; 54, Medway, 1970; 55, Struhsaker, 1975; 56, Rapaport and Mellen, 1990; 57, Jay, 1965; 58, Burton et al., 1995; 59, San Francisco Zoo; 60, Portland Zoo; 61, Poirier, 1969; 62, Islam and Husain, 1982; 63, Rudran, 1973; 64, Fossey, 1979; 65, Goodall, 1965, 1986; 66, Rijksen, 1978; 67, Hill, 1953; 68, Klopfer and Boskoff, 1979; 69, Tattersall, 1986; 70, Colquhoun, 1993; 71, Sussman, 1977; 72, C. Frederick, personal communication; 73, Hill, 1955; 74, Haring and Wright, 1989.

information. Some species have multiple entries when subspecies differed or subspecific information was available from only one source. Subspecific information is provided according to the nomenclature given by the source in question. If subspecific distinctions are absent in Tables 1 and 2,

data were lacking or all subspecies conformed to the specific pattern. Disagreements about taxonomic nomenclature were beyond the scope of this paper, so I rely on recent revisions whenever possible. Genera are treated conservatively (lumping more than splitting). One taxonomic debate bears



TABLE 3. *Coloration of gibbons (Hylobates spp.)*

Species name	Dorsal coloration				Notes on pelage	Infant contrast		Sources <sup>4</sup>
	Adult male	Adult female	Juvenile	Infant		To mother	To father	
<i>agilis</i> <sup>1</sup>	Buff or dark brown	Buff or dark brown	Variable	Variable	Infants have natal face ring	Varies	Varies	1–3
<i>concolor</i> <sup>2</sup>	Black	Fair	Black	Fair	Possibly asexually polychromatic	0	2	2–4
<i>hoolock</i>	Black	Fair	Black	Fair		0	2	2, 3, 5, 6
<i>klossii</i>	Black	Black	Black	Black		0	0	2, 7
<i>lar</i> <sup>3</sup>	Buff or black	Buff or black	Buff or black	Buff or black	Asexually polychromatic	Varies	Varies	2, 3, 8
<i>moloch</i>	Silver to grey	Silver to grey	Silver to grey	Silver to grey		0	0	2, 7
<i>muelleri</i>	Brown to grey	Brown to grey	?	Variable	Color varies without distinct phases	Varies	Varies	2, 3, 8
<i>pileatus</i>	Black	Grey to buff	Grey to buff	Grey to buff		0	2	1–3
<i>syndactylus</i>	Black	Black	Black	Black		0	0	2, 7

<sup>1</sup> *H.a. albibarbis* offspring become the same color as same-sex adults.

<sup>2</sup> *H.c. hainanus* adult females and infants range from cream to brown.

<sup>3</sup> *H.l. vestitus* range from buff to black without distinct phases.

<sup>4</sup> Sources: 1, Brockelman and Gittins, 1984; 2, Marshall and Sugardjito, 1986; 3, Mootnick, unpublished data; 4, Zhenhe et al., 1989; 5, Schilling, 1984; 6, Choudhury, 1990; 7, Preuschoft et al., 1984; 8, Groves, 1984.

mention. The taxa once referred to *Presbytis* have been subdivided among two or three genera (Oates et al. 1994). I side with E. Delson among the latter authors in viewing *Trachypithecus* as a subgenus of *Semnopithecus*. Furthermore, Oates et al. (1994) did not review Aimi and Bakar (1992), so the differences between *Presbytis femoralis* and *P. frontata* or *Trachypithecus obscurus* and *T. phayrei* remain ambiguous.

The analyses presented here risk statistical bias through the nonindependence of related populations (Harvey and Pagel, 1991). For example, *Papio* spp. and many *Cercopithecus* spp. form a cluster having blackish infants. Yet species which reverse generic trends can be found in several lineages (see Results). The question of phylogenetic constraint is treated primarily in the Discussion.

Survey data are cited by name of the captive facility. Quantitative data on allomothering are taken from Kohda (1985) and supplemented by field records. Data on testes weight are taken from Harcourt et al. (1995). Methodological differences preclude effective joining of the latter data set with another larger compilation for prosimian testes (Glander et al., 1992; Kappeler, 1993). Life-history parameters—female body weight (BW hereafter, in kilograms), neonate BW, age at weaning, and age at first breeding—

were taken from Harvey et al. (1987) and from Hill's publications (Table 2). Time spent by infants out of arm's reach of their mothers was taken from Treves (1996).

## RESULTS

### Distribution and development of natal coats

Twenty-six zoos and captive facilities responded to surveys (65%). Data are presented for 138 separate species (in 168 different entries) in Tables 2 and 3. Coloration of gibbons (*Hylobates* spp.) is treated separately because infants were often variable in color and sources were not always consistent (Table 3). A small percentage of entries was questionable or contradictory between sources (for contrast with mothers 16.1%, fathers 15.5%). The remainder are referred to as *confirmed* hereafter.

Infants were sexually dichromatic or asexually polychromatic in 6 (3.5%) confirmed entries (*Pithecia pithecia chryscephala*, *Eulemur* (*Petterus*) *macaco flavifrons*, *E. m. macaco*, *Hylobates agilis*, *H. lar*, and *H. muelleri* (Tables 2, 3). Within 17 of 138 (12.3%) species, subspecies differed in natal coat contrast. When data from Tables 2 and 3 are combined, 66 (46.8%) confirmed entries had infants with category 0 contrast (no difference) to the mother; 61 (42.9%)

were similar to the father. Fifty-one confirmed entries (36.2%) had infants with category 1 contrast (inconspicuous) to their mothers (36.6% when compared to their fathers). Less than one-fifth of all species sampled had category 2 natal coats (flamboyant: 14.2% when compared to mothers, 17.6% when compared to fathers).

Gibbons are tabulated separately, as infant color varied unpredictably in some species (Table 3) (Mootnick, personal communication). In general, if the immature gibbon coat differed from the adult, it tended to resemble the mother during the infant stage (<1 year) and the father during the juvenile stage (2–4 years) (Marshall and Sugardjito, 1986; Schilling, 1984; Zhenhe et al., 1989). As a result, in gibbon species with sexual dichromatism, the female changed from adult female color to adult male color and back to adult female color during her development.

Because subspecies are often identified on the basis of consistent color differences (Fooden, 1969, 1987; Groves, 1970, 1980; Medway, 1970), it would not be surprising if infant coloration and contrast with adults varied between subspecies. Several of the species displaying discrepancies in records are subspeciose. For example, Hershkovitz (1987a) recently documented the variability in coat color of the subspecies of the white-faced saki (*Pithecia pithecia*), and this species produced some contradictory surveys (Table 2).

Humans (*Homo sapiens*) are excluded from Table 2 but appear to conform to the great ape pattern in having no natal coat. However, reports of infants of European ancestry born with dark or pale fetal pelage (lanugo) or head hair replaced by a different color require more study (Kitzinger, 1980; Nilsson and Hamberger, 1990).

The age at which natal coats began to change and/or the age at which the change ended were available for 42 species in 51 entries (Table 4). Excluding the data points which refer to time required to reach adult male color (*Alouatta caraya*, *Pithecia pithecia*), the average age at which the natal coat began to change was 8.4 weeks (range = 1.5–52,  $N = 19$ ). Excluding the outlier of *Cercopithecus neglectus* reported by source 18, the average dropped to 5.7 weeks. The average

age at which the natal coat had disappeared was 20.5 weeks (range = 4–104,  $N = 40$ ). Again excluding the *C. neglectus* outlier, the average dropped to 18.0 weeks.

When categories of contrast to each other were compared, clear differences emerged. Some respondents provided the timing of change of infant pelage which did not contrast (0 = change due to texture, length, or minor differences but not contrasting coloration: start = 4.5 weeks, end = 9.5 weeks). Thus, the infants who were similar to adults underwent the change to adult pelage rapidly and far earlier than infants who contrasted with adults (completing change at 21 weeks). Among infants who contrasted, those with flamboyant (category 2) coloration began to change much earlier (3.2 weeks) than those with inconspicuous (category 1) coloration (14.2 weeks), but the two types of infants lost natal coloration at almost identical ages (20.7 vs. 22.1 weeks, respectively). This was true even if the questionable contrasts of Table 4 are set to their minimum or maximum values. The earliest onset of change occurred in *Pygathrix (Rhinopithecus) roxellana*, and the latest retention of a natal coat was reported for *Cercopithecus neglectus*. This is liable to reflect intensity of observation, however.

There was no evidence that relevant life-history parameters could predict the timing of loss of the natal coat. Neither adult female body weight (BW), neonatal BW, nor age at first breeding was correlated with the age at which the natal coat began or completed its transformation (statistics for completed age: Spearman rho: female BW  $N = 39$ ,  $Z = 1.4$ ,  $P = 0.16$ ; neonate BW  $N = 27$ ,  $Z = -1.2$ ,  $P = 0.24$ ; first breeding:  $N = 19$ ,  $Z = 0.1$ ,  $P = 0.95$ ). Finally, the age at which infants spent approximately one-fourth of their time out of arm's reach of the mother (Treves, 1996) was statistically indistinguishable from the age at which the natal coat disappeared (Wilcoxon signed-ranks test:  $N = 12$ ,  $Z = -1.3$ ,  $P = 0.18$ ). Because the data sets are small for life-history and developmental indices, these results must be regarded as preliminary. Moreover, there is certainly the possibility that published life-history indices are inaccurate (e.g., compare Oates et al. [1994] to Harvey et al. [1987]).

TABLE 4. *Natal coat duration and pattern of change*

Species	Contrast <sup>1</sup>	N <sup>2</sup>	Change (weeks)		First body part to change	Notes and sources from Table 2
			Begins	Ends		
<i>Alouatta caraya</i>	0	3	56–60	156	Dorsal	Describes male change to adult color: 2–4
<i>A. palliata</i>	1	na		12		5
<i>A. pigra</i>	1	2		7–9	Dorsal, head	6
<i>A. seniculus sara</i>	1	2		8		7
<i>Ateles geoffroyi geoffroyi</i>	2	3	3	12–16	Head, limbs	12, 13
<i>Lagothrix lagotricha poeppigii</i>	0	1	5	8	Dorsal	Loss of natal pelage but no contrast: 23
<i>Pithecia pithecia pithecia</i>	1	1	2	6	Ventral	12
<i>P. p. subspecies?</i>	0	na	18–20	126–168	Dorsal	Describes male change to adult male color: 25
<i>Cercocebus galeritus agilis</i>	0 or 1	2	3	6–8	Dorsal, ventral	12
<i>C. g. chrysogaster</i>	1	2	2	28	Ventral, head	29
<i>C. torquatus torquatus</i>	0 or 1	2		8	Head	7
<i>Cercopithecus aethiops</i>	1 or 2	na		18		30
<i>C. a. tantalus</i>	2	na			Forehead	31
<i>C. a. sabaeus</i>	2	na		64–68	Face, forehead	31
<i>C. ascanius schmidtii</i>	1	5	3	12	Tail, dorsal	32
<i>C. diana diana</i>	0 or 1	na		4–6	Hind limbs, rump	13
<i>C. hamlyni</i>	2	na		16		31
<i>C. lhoesti</i>	1	1		11		31
<i>C. neglectus</i>	1	2	52	104	Brow, rump	18
<i>C. neglectus</i>	1	na		36		31, 34
<i>C. wolffi</i>	0	2	4	10–12		Loss of natal pelage but no contrast: 12
<i>C. (Erythrocebus) patas</i>	2	2	3	4	Dorsal, head	18
<i>C. (E.) patas</i>	1	75	2–3	7–14	Tail	36, 38
<i>C. (E.) patas patas</i>	2	na	12	24		37
<i>C. (Allenopithecus) nigroviridis</i>	0	na		9.5	Head	31
<i>Colobus guereza kikuyensis</i>	2	5	2.3	16–17+	Head, shoulders	21
<i>C. polykomos polykomos</i>	2	7	1.9–3.9	12–16	Head, dorsal	17, 42
<i>Macaca arctoides</i>	2	na	4	28–52	Dorsal	28, 44
<i>M. fuscata</i>	0 or 1	1	16	20		28
<i>M. silenus</i>	1	3			Head	Infant lacks mane, tail tuft, hair on chest: 16
<i>M. sylvanus</i>	?	na		24		41
<i>Mandrillus leucophaeus</i>	1	1	20	36	Head	7
<i>Papio cynocephalus</i>	1	11		24		51
<i>P. hamadryas</i>	1	2	16–20	24–40	Dorsal, head	18, 41
<i>P. papio</i>	1	3		24+	Dorsal, head	15
<i>Presbytis rubicunda</i>	2	1			Dorsal, tail	33
<i>Procolobus badius rufomitratus</i>	1	na		10		40, 55
<i>P. b. tephrosceles</i>	1	10+		14		40, 55
<i>Semnopithecus cristatus ultimus</i>	2	2			Head, tail	21
<i>S. entellus</i>	2	na		12–20	Crown, head, beard	57
<i>S. francoisi</i>	2	5	2–5	20–32	Head, limbs	29, 52, 58–60
<i>S. johnii</i>	1 or 2	na		10–14		61
<i>S. obscurus</i>	2	6	5–6	17	Tail, dorsal	15
<i>S. vetulus</i>	1	2		12–16		13
<i>Pygathrix roxellana</i>	2	1	1.5	3+	Cheeks, outer arms	56
<i>Theropithecus gelada</i>	1	2			Head	7
<i>Hylobates concolor subspecies?</i>	0	na		52	Hands, feet	See Table 3
<i>H. c. hainanus</i>	0	3+		104		See Table 3
<i>H. hooleck</i>	0	na				See Table 3
<i>H. pileatus</i>	0	na			Chest, crown	See Table 3
<i>Nycticebus coucang</i>	1	na		11		46

<sup>1</sup> Natal coat contrast to mother (see Table 2).<sup>2</sup> Sample size of infants contributing data.

The body parts reported to change earliest were most often the dorsal portions or the head of the infant (Table 4). Because sources typically identified more than one body part as the first to change, the sample size here is 54 body parts (mentioned in 33 entries). In 21 of the 54 (39%), the head was one of the first body parts to lose natal pelage. In 15 of 54 (28%), the dorsal surface was one of the first. Combined, the first body part to change was either the head or dorsal areas in 91% (30 of 33) of entries. In only 15% of entries were limbs mentioned as first to change, 12% reported the tail, and 12% reported the ventrum (percentages do not total 100% because several body parts were reported as first to change in many surveys).

Because most of the data described in the preceding paragraph derive from captive studies, it is unlikely that the observed pattern is due simply to those body parts being the easiest to observe when the infant is clinging to the ventral surface of the mother. Horwich and Gebhard (1986) and Mearns and Pidgeon (1978) describe in detail the change in coloration of *Alouatta pigra* and *Colobus polykomos*, respectively. Their full descriptions support the generalization that head and dorsal parts are typically the first to lose the natal coloration.

#### Tests of the functional hypotheses

The alloparental hypothesis predicts that the natal coat releases alloparental care. Contrast with the maternal coat is therefore the relevant measure, not the intensity of the contrast. Accordingly, presence or absence of a natal coat was tested against alloparenting (Table 5), but no significant association was found ( $N = 52$ , Fisher's exact  $P = 0.99$ ). Even if the questionable values are included, there is no significant association (set to lowest value:  $P = 0.99$ ; set to highest value:  $P = 0.52$ ).

Simple presence or absence may be inadequate to describe alloparenting, so more detailed data were used (Table 5). Excluding questionable values, there was no significant effect of percent of time (Mann-Whitney U test:  $Z = -0.8$ ,  $P = 0.40$ ) nor mean duration of bouts ( $Z = -1.1$ ,  $P = 0.26$ ) spent with alloparents. Including the questionable values had no effect on either result.

The infant defense and paternity cloak hypotheses predicted opposite patterns of natal coat evolution depending on mating system. Relative testes weight was used as the indicator of promiscuity in mating systems to distinguish the two hypotheses (Table 6). Because infant defense treats flamboyant natal coats differently from inconspicuous coats, the following tests separate category 1 from 2.

Natal coat contrast values and testes weight values were available for 51 species, but ten were excluded as questionable (Table 6). The contrast with the mother was used to test the infant defense hypothesis, while the test of paternity cloak required the contrast with the father. Only *Papio hamadryas* shows sexual dichromatism in this data set (Table 6). With confirmed entries only used, natal coat contrast categories differed significantly in mean testes weight (Fig. 1) (Kruskal-Wallis  $H = 8.0$ ,  $P = 0.018$ ). Inconspicuous natal coat contrasts (category 1) were associated with the highest relative testes weights, whereas flamboyant natal coat contrasts (category 2) were associated with the lowest relative testes weights. Species with no natal coat (category 0) lay intermediate to the others (Fig. 1). Recalculating using contrast 2 for *P. hamadryas* did not change the results ( $H = 7.8$ ,  $P = 0.019$ ).

Underlying the relationship depicted in Figure 1 may be phylogenetic clustering due to shared ancestry. *Papio* and *Cercopithecus* species have inconspicuous infants usually and higher testes weights than the Colobinae, which tend to have flamboyant infants. This suggests that subfamilies are not independent replicates for such analyses (contra Harcourt et al., 1995). However, several reversals within clades indicate that relative testes weight does respond to mating system independent of shared ancestry (e.g., *Papio hamadryas*, *Pan troglodytes*, *Cercopithecus aethiops*, *Miopithecus talapoin*). In fact, three reversals support the hypothesized link between natal coat contrast and mating system. Among the Colobinae, *Nasalis larvatus* has no natal coat (Table 6), and its residual for testes weight is substantially higher (residual =  $-0.281$ ) than the other members of its subfamily (Colobinae excluding *Nasalis*,  $N = 5$ , residual =  $-0.416$ ).

TABLE 5. Occurrence and intensity of alloparental care in relation to infant natal coat contrast

Species	Alloparental care			Source <sup>4</sup>
	Present?	% time <sup>1</sup>	Duration <sup>2</sup>	
<i>Alouatta palliata</i>	No	0	0	1
<i>A. pigra</i>	Yes	3	3	2
<i>A. seniculus</i>	No	0	0	3
<i>Aotus trivirgatus</i>	Yes	33.5	11.9	1
<i>Ateles geoffroyi</i>	No	0	0	1
<i>Brachyteles arachnoides</i>	No	0	0	1
<i>Callicebus moloch</i>	Yes	3	3	1
<i>C. torquatus</i>	Yes	3	3	1
<i>Callimico goeldi</i>	Yes	52	10.6	1, 4
<i>Callithrix jacchus</i>	Yes	72.4	16.7	1, 4
<i>Cebuella pygmaea</i>	Yes	57	11.4	1, 4
<i>Cebus albifrons</i>	No	0	0	1
<i>C. apella</i>	No	0	0	1
<i>C. capucinus</i>	No	0	0	1
<i>C. olivaceus</i>	Yes	3	3	5
<i>C. torquatus atys</i>	No	0	0	1
<i>Cercopithecus aethiops</i>	Yes	2.7	4.3	1
<i>C. ascanius</i>	Yes	3	3	6
<i>C. neglectus</i>	No	0	0	1
<i>Colobus guereza</i>	Yes	29.7	3	1
<i>C. polykomos</i>	Yes	22.2	3	1
<i>C. (E.) patas</i>	Yes	0.5	0.5	1
<i>Eulemur fulvus rufus</i>	No	0	0	7, 8
<i>Gorilla gorilla</i>	No	0	0	9
<i>Lagothrix lagotricha</i>	No	0	0	1
<i>Lemur catta</i>	Yes	3	3	7
<i>Leontopithecus rosalia</i>	Yes	3	3	1
<i>Lophocebus albigena</i>	No	0	0	1
<i>Macaca cyclopis</i>	No	0	0	1
<i>M. fascicularis</i>	Yes	4.1	1.7	1
<i>M. fuscata</i>	No	0	0	1
<i>M. mulatta</i>	No	0	0	1
<i>M. nemestrina</i>	No	0	0	1
<i>M. radiata</i>	No	0	0	1
<i>M. sylvanus</i>	Yes	3	3	10, 11
<i>M. thibetana</i>	Yes	3	3	12
<i>Mandrillus leucophaeus</i>	No	0	0	1
<i>Nasalis larvatus</i>	Yes	0.3	1.8	1
<i>Pan troglodytes</i>	No	0	0	13
<i>Papio anubis</i>	Yes	0.8	6	1
<i>P. hamadryas</i>	No	0	0	1
<i>Presbytis melalophos</i>	No	0	0	14
<i>Procolobus badius</i>	No	0	0	6, 15
<i>Propithecus diadema</i>	Yes	3	3	16
<i>P. verreauxi</i>	Yes	3	3	8, 16
<i>Saguinus fuscicollis</i>	Yes	3	3	1
<i>S. labiatus</i>	Yes	69.3	13.4	1
<i>S. mystax</i>	Yes	3	3	1
<i>Saimiri boliviensis</i>	Yes	3	3	17
<i>S. sciureus</i>	Yes	43.4	7.6	1
<i>Semnopithecus (T.) cristatus</i>	Yes	24.9	4.3	1
<i>S. entellus</i>	Yes	3	3	1
<i>S. (T.) francoisi</i>	Yes	22	4.6	1
<i>S. (T.) johnii</i>	Yes	3	3	1
<i>S. (T.) obscura</i>	Yes	3	3	1
<i>S. (T.) vetulus (senex)</i>	Yes	3	3	1
<i>Theropithecus gelada</i>	No	0	0	1
<i>Varecia variegata</i>	Yes	3	3	18

<sup>1</sup> Percent of time dependent infant spends in alloparental care (Kohda, 1985).<sup>2</sup> Duration (minutes) of bouts of alloparenting (Kohda, 1985).<sup>3</sup> Not available using the methods in Kohda (1985).<sup>4</sup> Sources: 1, Kohda, 1985; 2, Horwich and Gebhard, 1986; 3, Sekulic, 1981; 4, Goldizen, 1987; 5, O'Brien and Robinson, 1991; 6, Treves, personal observation; 7, Sussman, 1977; 8, Klopfer and Boskoff, 1979; 9, Fossey, 1979; 10, Taub, 1980; 11, Small, 1990; 12, Fooden et al., 1985; 13, Goodall, 1986; 14, Curtin, 1976; 15, Struhsaker and Oates, 1975; 16, Grieser, 1992; 17, Williams et al., 1994; 18, Pereira et al., 1987.



TABLE 6. The residual of testes weight (g) on body weight (kg) in relation to natal coat contrast

Species	Testes weight residual <sup>1</sup>	Natal coat contrast	Species	Testes weight residual	Natal coat contrast
<i>Alouatta palliata</i>	0.25	1	<i>Lophocebus aterrimus</i>	-0.064	0
<i>Aotus trivirgatus</i>	-0.476	0	<i>Loris tardigradus</i>	0.078	0 or 1
<i>Ateles geoffroyi</i>	-0.01	1 or 2	<i>Macaca arctoides</i>	0.466	2
<i>Avahi laniger</i>	-0.304	1	<i>M. fascicularis</i>	0.575	1
<i>Cacajao calvus</i>	-0.137	0 <sup>2</sup>	<i>M. mulatta</i>	0.487	1
<i>Callithrix argentata</i>	0.003	0	<i>M. nemestrina</i>	0.622	1
<i>C. jacchus</i>	-0.112	0	<i>M. radiata</i>	0.521	1
<i>Cebuella pygmaea</i>	-0.452	0	<i>Mandrillus leucophaeus</i>	0.214	1
<i>Cebus apella</i>	-0.195	0 or 1	<i>M. sphinx</i>	0.274	0 or 1
<i>Cercocebus torquatus atys</i>	0.237	0	<i>Microcebus murinus</i>	0.602	0
<i>Cercopithecus aethiops</i>	0.111	1 or 2	<i>Nasalis larvatus</i>	-0.281	0
<i>C. ascanius</i>	-0.549	1	<i>Pan troglodytes</i>	0.513	0
<i>C. (A.) nigroviridis</i>	0.223	0	<i>Papio cynocephalus</i>	0.36	1 <sup>3</sup>
<i>C. (E.) patas</i>	-0.346	1 or 2	<i>P. hamadryas</i>	0.031	1 or 2
<i>C. (M.) talapoin</i>	0.103	0	<i>P. papio</i>	0.416	1
<i>Cheirogaleus major</i>	0.119	0 or 1	<i>Pongo pygmaeus</i>	-0.217	0
<i>Colobus guereza</i>	-0.74	2	<i>Presbytis rubicunda</i>	-0.537	2
<i>C. polykomos</i>	-0.181	2	<i>Semnopithecus cristatus</i>	-0.292	2
<i>Eulemur (P.) fulvus</i>	0.082	0	<i>S. entellus</i>	-0.308	1 or 2
<i>Galago demidovii</i>	0.135	0 <sup>2</sup>	<i>S. obscurus</i>	-0.438	2
<i>G. senegalensis</i>	0.101	0	<i>Saguinus midas</i>	-0.127	0 or 1
<i>Gorilla gorilla</i>	-0.578	0	<i>S. nigricollis</i>	0.245	0
<i>Homo sapiens</i>	-0.13	0	<i>S. oedipus</i>	0.168	0
<i>Hylobates moloch</i>	-0.245	0	<i>Saimiri sciureus</i>	0.026	0
<i>Lagothrix lagotricha</i>	0.031	0	<i>Theropithecus gelada</i>	-0.172	1
<i>Leontopithecus rosalia</i>	-0.209	0 or 1	<i>Varecia variegata</i>	0.243	0

<sup>1</sup> Residual of the regression of log(testes weight) on log(female body weight) taken from Harcourt et al. (1995).

<sup>2</sup> Two missing values (*Cacajao calvus*, *Galago demidovii*) were replaced with congeners (*C. melanocephalus*, *G. moholi*).

<sup>3</sup> Contrast to mother and father differ.

Similarly, among the macaques, *M. arctoides* has flamboyant infants and small testes (residual = +0.466) compared to the remaining species which have inconspicuous infants and larger testes (excluding *M. arctoides*,  $N = 4$ , residual = +0.551). This suggests that shared ancestry does not explain all of the relationship between mating system and natal coats. But caution is indeed warranted until more data on testes weight are available.

## DISCUSSION

This paper presents the first compilation of information on primate natal coat distribution, duration, and molt pattern. The compilation and analysis must be regarded as preliminary because many species had ambiguous values or were absent from the data set, and the pictorial guides used to code natal coat contrast did not provide rigorous quantification. For example, the Lemuroidea and Ceboidea were underrepresented, and information on subspecific, regional, or interpopulational differences is sorely lacking. As a result, the instances in which

subspecific variation is indicated (*Loris tardigradus*, *Cebus apella*, *Cercopithecus mitis*, among others) cannot be fully evaluated.

Approximately half of the species displayed no contrast between infant and adult coloration. The absence of contrasting natal pelage was most common among New World monkeys. Contrasting infant pelage was more common in the Old World Cercopithecidae but absent from the great apes. The lesser apes (*Hylobates* spp.) contained several species with pelage differentiation. Prosimian taxa displayed a tremendous variety of patterns. Flamboyant coats were most common among the Colobinae, while inconspicuous contrast was most common among the noncolobine Cercopithecidae. This dichotomy once led to speculations about the role of folivory in the evolution of flamboyant coats and alloparenting (McKenna, 1979; Quiatt, 1979).

At the individual level, the change from natal to juvenile pelage was most likely to begin with the dorsal surface and/or the head. Typically, change ended long before weaning and began around the period when



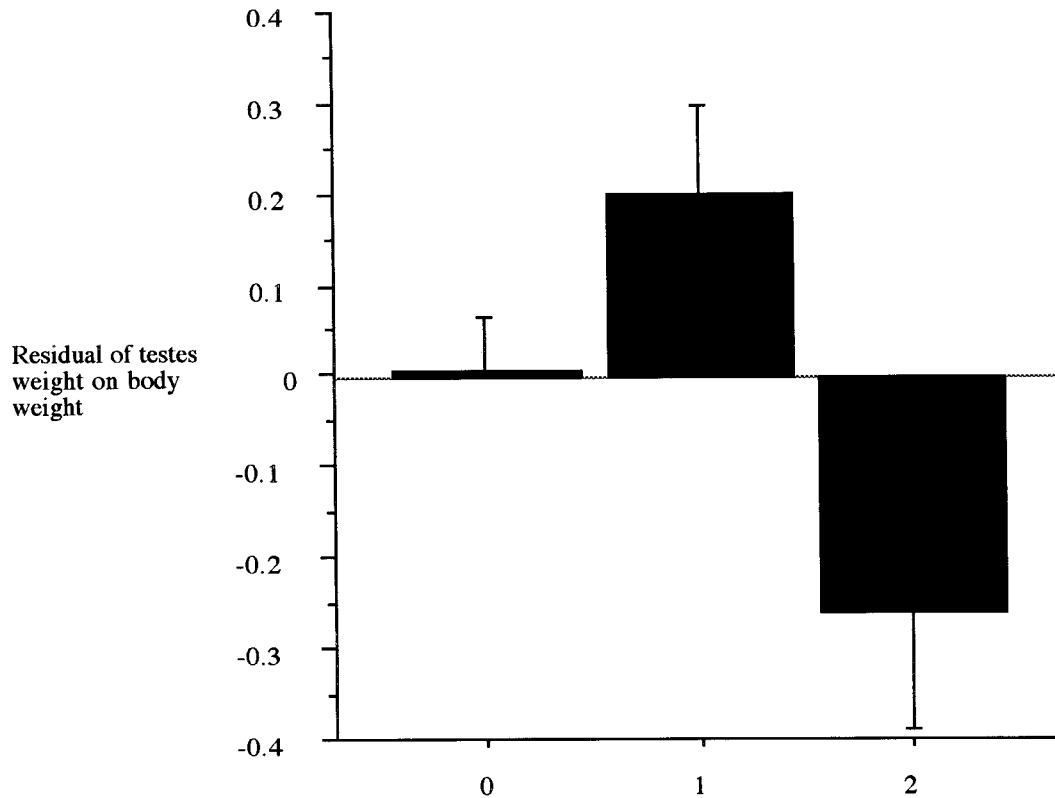


Fig. 1. Relationship of relative testis weight to natal coat contrast. Y axis: residuals of the regression of testis weight (g) on body weight (kg). X axis: 0, no contrast between infant and mother; 1, discreet; 2, flamboyant. Error bars depict one standard error ( $P < 0.02$ ). Questionable species were excluded (see Results).

the infant spent substantial (~25%) time out of arm's reach of its mother. The close link between infant independence and natal coat loss was noted 30 years ago (Gartlan and Brain, 1968). This may support the expectation that risk to infants increases with increased independence (Hrdy, 1976; Treves, 1996). Hrdy (1976) suggested that some species' natal coats were not flamboyant because of predation pressure. Although flamboyant coats began to change earlier than natal pelage of inconspicuous contrast, the two types of coat disappeared completely at approximately the same average age. The pelage changes in species without natal coats (category 0 changes in pelage thickness and texture) were completed more rapidly than the transformation of natal coats into adult coloration, also contradicting the presumed relationship with predation risk.

Bearing in mind the diverse sources of information and the subjective nature of the color contrast coding being used, there is remarkable consistency between sources and species in the timing and pattern of developmental change in color. This provides greater confidence in the data set and allows a preliminary assessment of the function of natal coats.

#### The function of natal coats

Natal coats are widespread in primates, and I found no evidence that neonates were ever observed without natal coats in the species displaying this trait. This suggests that the genetic system underlying natal coats rapidly evolves to fixation within populations, reflecting strong selection on the trait. The perspective taken in this paper has therefore been adaptationist (i.e., no

nonfunctional hypotheses were examined). Phyletic constraints on natal coats are discussed in subsequent sections.

Evolutionary scenarios for the selective advantage of natal coats are still in their infancy. In the following section, the three functional explanations for natal coats are examined.

First, the alloparental hypothesis originally formulated by Hrdy (1976) predicted that species with nonmaternal care of the infants would evolve natal coats as a trigger or release of care for the infant. The link between alloparenting and natal coats was suggested because of the intense interest displayed to neonates by other group members in certain species coupled with the dramatic decrease in interest after loss of the natal coat (Horwich and Gebhard, 1986; Hrdy, 1976; Oates, 1977). However, no statistical association between alloparenting and presence of a natal coat could be detected in this study. Moreover, the natal coat was replaced long before the infant reached independence. Overall, the alloparental hypothesis found no support from the present analyses. This should not be misconstrued: abundant evidence exists to support the claim that interest in neonates declines with loss of the natal coat. The present analysis suggests only that alloparental care is not the selective advantage favoring the evolution of the coats. The role of infant transfer in cooperative coalitions and kin group cohesion remains unquestioned. Furthermore, the role of alloparental care in the behavioral complex of infant natal coats is entirely compatible with both of the infanticide-avoidance explanations tested.

Second, the infant defense hypothesis suggested that natal coats evolved as signals to deter threatening adult males. By reliably signaling its presence, the neonate also communicates the potential resistance which unfamiliar males will face in approaching a kin group containing an infant. In this view, bright natal coats signal males outside of groups, while inconspicuous yet distinct coats are sufficient to signal males peripheral to the kin group (i.e., unrelated group members). Functional arguments about signal design suggest that the most visible portions would produce the signal most effectively

and should therefore be maintained for the longest period. Contrary to the expectations of this hypothesis, the first body parts to change were those most detectable when the infant is clinging to the mother (dorsum and head). However, this hypothesis correctly predicted the presence of two functionally differentiated categories of natal coat.

The paternity cloak hypothesis predicted that infants face a selective disadvantage if they display phenotypic cues to paternity in social systems where females have copulated with many males. Support for this hypothesis comes from the body parts changing first: the head and dorsum are least open to phenotypic matching and therefore least usable by males to exclude themselves as probable fathers. Adult sexual dichromatism occurred in several species, but in only two cases were infants sexually dichromatic. In support of paternity cloak, infants were more likely to differ from the adult male than the adult female color.

### The evolution of natal coats

The current analysis provides a foundation for future functional analyses and hints at a selective pressure for the evolution of natal coats. The alloparental hypothesis received no support, indicating that neither the mere fact of alloparental care nor its intensity was associated with natal coats in infants. The other functional hypotheses, infant defense and paternal cloak, received equivocal support. On the one hand, infant defense predicted two distinct coat contrast patterns, while, on the other, paternity cloak provided the best predictions for which body parts changed first (Table 1). Neither hypothesis taken alone perfectly predicted the relationship between adult male testes weight and infant natal coats across species. In fact, the observed association between testes weight and the natal coat requires careful scrutiny.

The infant defense hypothesis did not predict a strong association of promiscuous mating systems with natal coats, because males who have mated with females are considered to be lesser infanticide risks (e.g., compare mortality in baboons [Collins et al., 1984] to that reported for gorillas [Watts, 1989]). The paternity cloak hypothesis did

not predict that natal coats would appear in species with small testes relative to body size. The two infanticide-avoidance hypotheses are only partially mutually exclusive (Table 1). Can they be integrated?

If natal coats function both as paternity confusion and warnings to unrelated males, the pattern observed in Figure 1 may be explainable. Groups with promiscuous mating, in which infants are exposed to many males at close quarters, require both paternity confusion and clear signals that infants will be defended from conspecific threat. Societies with one-male groups and extra-group copulations will require bright signals for longer-distance communication as well as paternity confusion to avoid discrimination by the resident male against nonkin infants. The intermediate societies (multi-male with nearly exclusive mating [Boinski, 1987; Janson, 1984]) or single-male with frequently promiscuous breeding [Richard, 1974]) will display an inconsistent pattern of natal coat expression (e.g., *Cebus apella*) depending on infant exposure to males and the degree of paternal investment. These factors may vary with demography; hence, subspecific differences could arise over time. Further research is needed to determine the interaction of mating systems and infanticide or its avoidance.

The combination of infanticide-avoidance hypotheses can predict the categorical difference between the two types of natal coats, the anatomical pattern of coat color change, and the importance of mating system. They were less successful in predicting the timing of change. All three hypotheses predicted longer maintenance of the natal coat than was observed. The predictions of the infanticide-avoidance hypotheses (Table 1) were closer to the actual duration of the natal coats than the alloparental hypothesis. In most species, infants are vulnerable to conspecific attack beyond the average 20 weeks of natal coat duration (Clarke, 1983; Crockett and Sekulic, 1984; Hrdy, 1977; Valderama et al., 1990) and may even be killed as juveniles (Rajpurohit and Sommer, 1991; Shopland, 1982). In five groups of Hanuman langurs (*Semnopithecus entellus*) which suffered takeovers by nongroup males, 11 out of 19 infants died or disappeared. Nine of the

11 were under 20 weeks old (Sommer and Mohnot, 1985). Thus, they still had all or remnants of their natal coats (Table 4). In sum, infanticide may strike immatures who have outgrown their natal coats, but the vast majority are killed while in natal pelage.

These data would seem to suggest that the natal coat does not protect infants, at least among Hanuman langurs, but information is needed on the success of infant defense at different ages. If young infants are defended more efficiently than older infants who are losing their natal coats (e.g., because the young infants are eye-catching), an infanticide-avoidance hypothesis would receive support. Unfortunately, data on the success and failure of females in defending their infants and their allies' infants are completely lacking. In fact, a widespread misconception that female coalitions are ineffective may have subtly hampered study of this question. Sommer (1987) reports that one-third of female coalitions consist of six to eight females other than the mother, and these coalitions may be quite successful in defending infants from infanticidal males (see also Treves and Chapman, 1996). In turn, if infant natal coats enhance female coalitionary action, infant survival may be increased. In this manner, the relationship of allomaternal care to natal coats may be reconciled with the infanticide-avoidance hypotheses tested in this paper.

### Phylogenetic constraints

A major drawback to the tests of the functional hypotheses in this paper is the effect of shared ancestry on the distribution of natal coats. Figure 1 reveals that treating inconspicuous coats as less contrasting than flamboyant coats obscures the categorical distinction between the two types (i.e., a ranking is not appropriate). Does the categorical distinctiveness of the two types of natal coat simply reflect separate evolutionary histories or real functional differences?

Because the genera dominated by inconspicuous natal coat contrasts (*Cercopithecus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) often have multimale social systems, they also have large testes relative to body size. Similarly, the genera dominated by

flamboyant natal coat contrasts (Colobinae) often have single-male social systems and correspondingly small relative testes weights. Thus, flamboyant and inconspicuous natal coats seem to have arisen separately in the two lineages and perhaps did so under different selective pressures. However, subspecific differentiation in natal coat contrast noted in this paper hints that effects acting independently of phylogeny can shape pelage differences.

Ultimately, social structure and developmental indices reflect shared ancestry to some extent, so any interspecific comparisons of patterns of behavior or morphology which vary with social structure are likely to face confounding effects of phylogeny. Determining whether the findings of this study reflect phylogeny only or some mixture of phylogeny and social adaptation will require analysis of variation within species. But two patterns identified in this study argue against an overwhelming influence of phylogeny.

First, infant independence was closely linked to loss of the natal coat independent of life-history parameters, such as body size, which correlates with developmental speed and reflects shared ancestry (Harvey et al., 1987). In a separate analysis of primate genera, comparison of infant development revealed that exploration away from the mother was delayed in social systems with multimale groups (Treves, 1996). In conjunction with the findings of the present analysis, it seems that the mating system and/or conspecific threat from males has a strong influence on infant development independent of life-history parameters.

Second, shared ancestry did not predict natal coat contrast perfectly. Two species which reversed the trends of their subfamilies (e.g., *Macaca arctoides* and *Nasalis larvatus*) followed the association between testes size and natal coat contrast (see Results). A third species presents an intriguing case: *Papio hamadryas* has low testes weight relative to body size (Harcourt et al., 1995) but conforms to its generic pattern of having blackish infants. However, it is the only cercopithecoid in which infant contrast with the father and the mother differs. The social system of hamadryas baboons is often char-

acterized by cyclic separation and aggregation of one-male groups. Perhaps this social system requires infant defense signals against all-male bands and paternity cloak because of low levels of sneak matings (Kummer, 1968).

All three of the exceptional species listed above differ from their relatives in social system or display variable social groupings (Fooden, 1990; Kummer, 1968; Kummer et al., 1985; Yeager, 1990). Our understanding of the origins of social systems may still be too rudimentary to disentangle the selective pressures engendered by different grouping patterns. Nevertheless, *Macaca arctoides*, *Nasalis larvatus*, and *Papio hamadryas* demonstrate that testes size and natal coats are not strictly constrained by phylogeny.

### The physiology of pelage color

Coat color derives primarily from melanin-based pigmentation deposited in hair shafts. This pigmentary color differs from coloration derived from structural iridescence (e.g., butterfly scales) or from hemoglobin near the surface of the skin (e.g., baboon perineal redness [Hershkovitz, 1977]). The discussion of pelage which follows is restricted to pigmentary coloration.

Agouti (a banded pattern appearing grey-brown) is hypothesized to be the primitive color of primates and perhaps all mammals (Hershkovitz, 1977; Kingdon, 1988). Agouti is believed to represent a general protective coloration optimizing concealment in a variety of habitats and light regimes. Primates which are largely agouti include the pygmy marmoset (*Cebuella pygmaea*) and many nocturnal prosimians. Pelage which is lighter or darker than agouti may provide better concealment than agouti in certain, specific habitats, but it does not retain the general utility of the ancestral agouti, according to one view (Hershkovitz, 1977).

Agouti is produced by alternating black (melanistic) and reddish (erythristic) banding on hairs. Variation in pelage color within populations is typically due to genetic and developmental differences in the number or type of melanin bands on hair shafts. For example, a study of hundreds of *Macaca arctoides* specimens revealed that 13% of individuals were blackish (melanistic) and

8.7% were reddish-brown (erythristic), while the majority of the population was brownish (Fooden, 1990).

HersHKovitz (1977) has hypothesized that two biochemical pathways for changes in hair color are possible and irreversible (the metachromism hypothesis hereafter). According to this hypothesis, if the reddish bands are reduced in number, pelage color will undergo a transformation from agouti to dark brown (black with a little red). If the depigmentation continues on this pathway, all red bands will be lost, yielding black. If depigmentation continues, black bands will be lost, and the hair will turn dark grey (black alternating with colorless hair). This progressive loss of pigmentation can lead to light grey, silvery, creamy, and finally colorless hair. On the other hand, if black bands are lost first, pelage color will undergo a transformation from agouti to red-brown (red with a little black). If depigmentation continues, the pelage will become red, and beyond this point red bands will be lost, yielding orange, gold, straw, cream, and finally colorless hair, converging on the other pathway with complete loss of melanin bands. The directions of change indicated above are invariant: all metachromic changes are from pigmented to less pigmented, never the reverse (HersHKovitz, 1977). Support for this idea comes from the common loss of color in captive animals, leading to pelage which is less black or less red (Haring and Wright, 1989; HersHKovitz, 1977).

The metachromism model of color change therefore predicts that any selection for a coat color change can lead only toward less agouti-like pelage. I am aware of no tests of this idea, but if it is validated, the metachromism hypothesis could provide a powerful tool for the analysis of age-related pelage differences. For example, infant Francois' leaf-monkey (*Presbytis francoisi*) are burnt orange, while the adults are black. The metachromic hypothesis suggests that black is closer to the ancestral agouti, while orange colors derive from nearly complete loss of black bands and partial loss of red bands. If change is truly unidirectional, one might infer that natal coats in this species are derived traits, not ancestral colors from which the adult form is derived.

In the majority of cases, inconspicuous contrasts arise from dark infant pelage (suggesting a loss of red pigment bands), while flamboyant contrasts arise from bright infant pelage (suggesting a loss of black pigment bands). Exceptions exist, however (*Semnopithecus entellus*). If natal coats function as infant adaptations to create contrasts with adults, they must be derived from the adult coloration. Therefore, searching for a function of the natal coat may produce spurious results when the adult coloration is the derived state. At present, the data are too gross and color comparisons too subjective to allow for an assessment of color derivation in most species. Hopefully, future interest will be sparked and quantitative measures of reflectance or pelage micro-anatomy will allow us to assign derived or ancestral character states to pelage with little ambiguity.

Contrasting natal coats are not restricted to primates. Molting during development is common among mammals (HersHKovitz, 1977), but instances where infants have sharply contrasting coloration when compared to adults are rarer. Spotted hyenas (*Crocuta crocuta*) and golden jackals (*Canis aureus*) have dark infants (Goodall and van Lawick, 1970). Tapir (*Tapirus* spp.) infants are striped (personal observation). Cheetah (*Acinonyx jubatus*) cubs have natal coats which change at 10 weeks, comparable to primate natal coats (Frame and Frame, 1980). For some or all of these animals, the infant coloration may relate to different anti-predator defense systems. This function has not been widely examined in primates, but the evolution of infant-carrying in primates produces different selective pressures on mother and neonate.

## CONCLUSIONS

The information on coat color and development amassed here is of variable quality. Not only do the data points come from a variety of sources, sometimes contradictory, but the analyses rely on an uncalibrated categorization of color which is a graded, continuous variable. Nevertheless, several factors encourage confidence in the data. First, only one source suggested that infants within species varied unpredictably in con-



trast (some *Hylobates* [Mootnick, personal communication]); thus, the overall consistency of reports argues that we are examining a distinct trait which undergoes little change due to environmental influences. Second, most sources were in concordance using a pictorial trichotomy representing no contrast, inconspicuous, and flamboyant contrast. Third, the information used generally came from animals seen in good light by observers with an intimate knowledge of their subjects and blind to the functional hypotheses being tested. Certainly there are some data points which must be viewed with caution. The present analyses relied on confirmed records whenever possible.

The functional hypotheses tested in this paper sought a unitary explanation for natal coats in all primates. This objective was not met. First, there were phylogenetic constraints which were only partially offset. Also, variation in Old World monkeys was addressed most convincingly, while patterns of infant pelage in prosimian, hominoid, and platyrrhine taxa remain largely unexplained. Nevertheless, three categories of natal coat contrast were distinguishable on the basis of interspecific differences in testes size. This novel finding was predicted a priori by the infanticide-avoidance hypotheses and suggests that the mating system and patterns of relatedness between males and infants directly influence natal coat contrast via differential survival of infants. In sum, this study joins many recent treatments of primate behavior and evolution which emphasize the potent selective pressure of infanticide. Infant development, morphology, and behavior appear to evolve in response to conspecific threat.

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